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Nighttime Habitat Use and Movement of Two Anaxyrus Species in Southeastern Virginia

Olivia Windorf

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A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelor of Science in Biology from
The College of William and Mary

by

Olivia Windorf

Accepted for Honors

Matthias Leu, Advisor

Randolph Chambers

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Abstract

With amphibian populations declining throughout the world, it is crucial to understand their habitat use and movement in order to create appropriate and effective conservation plans. However, most studies do not look at amphibian behaviors during the night, leaving a large portion of amphibian activity understudied. In this study I researched the habitat use and movement of the American Toad, *Anaxyrus americanus*, which has stable populations and the Fowler's Toad, *Anaxyrus fowerli*, which is experiencing population declines. In the first chapter, I found that these species both use habitat similarly at night. However, they use open spaces rather than habitat that is useful to prevent desiccation and to hide as is normally documented in studies. This highlights the difference between nighttime and daytime habitat use. In the second chapter, I found that nighttime movement is affected by weather variables. Weekly weather patterns were more important for large movements away from the roost site, while smaller movements within the night were explained by daily weather variation. These results show the types of movements that are often missed by daily movement studies. It would be beneficial to consider the behavior of amphibian species over the course of a full day to create the most informed conservation plans.

Introduction

Amphibian populations are declining rapidly throughout the world. Worldwide since 1980, nine species have become extinct, 113 more are possibly extinct (Skerrat et al. 2007), and 43% of remaining species are experiencing some form of population decline (Rohr et al. 2011). Amphibians show the highest decline of all vertebrate taxa, with 20% more species threatened compared to birds and 10% compared to mammals (Stuart et al. 2004). Amphibian extinction rates are already around 200 times the historical background (Collins 2010, McCallum 2007). Within the United States, Adams et al. (2013) found that amphibian occupancy in ponds and other wetland habitat decreased 3.7% annually between 2002 and 2011. Even common species, such as Spring Peepers (*Pseudacris crucifer*) are experiencing population declines (Adams et al. 2013). Without intervention, species extinctions will continue to increase (Rohr et al. 2011).

The loss of amphibians has detrimental effects on ecosystems. At every life stage amphibians are an important part of an ecosystem's trophic system, with adult and juvenile amphibians as carnivores and prey in terrestrial systems and tadpoles as herbivores and prey in aquatic systems (Blaustein et al. 1994). As ectotherms, amphibians are efficient energy converters and therefore serve as important connections between high and low trophic levels (Hopkins 2007). In addition, amphibians are often used as indicator species for overall ecosystem health (Blaustein et al. 2003, Collins and Storfer 2003) due to their biphasic life cycle, which exposes them to aquatic and terrestrial stressors. In addition, their permeable skin and eggs leave them vulnerable to poor water quality and UV radiation (Blaustein and Kiesecker 2002). Degradation to the quality or size of aquatic and terrestrial habitats are reflected in amphibian populations (Hopkins 2007). Due to their vulnerability to a large range of stressors, many factors influence population declines. Some of these factors are described below.

Batrachochytrium dendrobatidis

Among multiple pathogens that affect amphibians, the skin pathogen *Batrachochytrium dendrobatidis* (*Bd*), which causes the disease chytridiomycosis, is the widely considered the most damaging to amphibian populations (Miller et al. 2018, Greshko 2018). In adult amphibians, this disease can cause excessive skin shedding, discoloration, lethargy, and death (Xie et al. 2016). The pathogen *Bd* may affect tadpoles by creating deformations in mouth structures, causing altered feeding (Xie et al. 2016). Likely originating in East Asia (O'Hanlon et al. 2018), though now established in every continent where amphibians are present (Morgan et al. 2007), chytridiomycosis has become a primary threat to amphibians, being found in more than 500 species (Miller et al. 2018). The ubiquity of *Bd* is caused by multiple factors including: the intentional and unintentional spread of amphibians through international trade (O'Hanlon et al. 2018, Rohr et al. 2011, Schloegel et al. 2012), human population density (Murray et al. 2011, Rohr et al. 2011), and increased vulnerability due to the detrimental effects of pesticide on amphibian immune systems (Davidson et al. 2007).

UV-B Radiation

As climate change worsens, stratospheric ozone decreases, the climate warms, and water, including smaller bodies of water such as lakes and ponds, acidify (Schindler et al. 1996, Blaustein et al. 2010). Water acidification lowers the amount of dissolved organic carbon in the water column, allowing for higher levels of UV-B penetration (Pahkala et al. 2002), which has led to a significant increase in UV-B radiation levels since 1979 (Blaustein et al. 2010). UV-B radiation affects amphibians more than other class of animal due to their permeable skin and eggs. In certain amphibian species, UV-B radiation causes mortality and decreased hatching success (Blaustein et al. 2010), in others it causes sublethal effects, which are nonetheless

damaging to individual fitness (Pahkala et al. 2001, Smith et al. 2000). Exposure to ambient UV-B radiation has been documented to delay metamorphosis and cause reduced mass in juveniles (Pahkala et al. 2001, Smith et al. 2000, Kaplan 1992). These sublethal effects are negatively correlated with future fecundity and survival (Pahkala et al. 2001, Kaplan 1992) and therefore have negative effects on overall population dynamics (Smith et al. 2000).

Invasive Alien Species

Invasive alien species cause population declines due to competition, predation, and sublethal but damaging effects on amphibian species that have no evolutionary history with the invasive alien species (Kats and Ferrer 2003). Predatory fish populations are the most common invasive alien species affecting amphibian populations (Stebbins and Cohen 1995). These fish are introduced into ecosystems for the purpose of recreational fishing (Collins and Storfer 2003) and biological control (Kats and Ferrer 2003). Mosquitofish (*Gambusia affinis*) introduced to control mosquito populations, trout and salmonids (*Salmo* spp.), introduced as game species, are all documented to cause amphibian population decline through predation on larvae (Beebee and Griffiths 2005, Gamradt and Kats 1996, Collins and Storfer 2003, Kats and Ferrer 2003). Introduced trout and salmonids are suspected to be the primary cause of multiple amphibian species declines in the western United States (Collins and Storfer 2003). These fish are decreasing amphibian populations beyond the area in which they are present, due to their effect on amphibian meta-populations (Beebee and Griffiths 2005). Introduced bullfrogs also cause native species declines through competition and predation (Kiesecker et al. 2001, Kats and Ferrer 2003). Amphibians raised in the presence of alien species have been found to be smaller as larvae and juveniles, likely as a physiological result of stress, ultimately affecting their future fitness (Kiesecker and Blaustein 1998, Lawler et al. 1999).

Pesticides and Herbicides

The effects of pollutants are especially relevant to amphibian species due to their use of terrestrial and aquatic habitats. Pesticides and herbicides are able to spread via air, rain, and surface water, leaving amphibians vulnerable at every stage of life (Sparling et al. 2001). Documented amphibian populations declines have been associated with populations downwind of agricultural fields (Davidson et al. 2004) due to suppressed immune functioning, delayed metamorphosis, and mortality. In addition, many herbicides, such as Atrazine, which has been found to cause feminization of amphibians, are applied during the spring when many species are breeding (Hayes et al 2002). This timing exposes larvae to these chemicals during important developmental stages. Many pesticides are also persistent pollutants. 25 years after the ban of DDx in the United States (a group of pesticides including DDT) amphibian population declines were still be attributed to the pesticides (Sparling et al. 2001).

Habitat Loss and Fragmentation

Habitat destruction is a primary concern for amphibian populations due their use of wetland and upland habitats. Upland habitat is experiencing a large degree of fragmentation due to development, while anthropogenic impacts, such as pollution, are greatly degrading the quality of wetlands (Jones and Tupper 2015). Amphibians are particularly vulnerable to habitat loss and fragmentation due to their low vagilitiy compared to mammal and bird species (deMaynadier and Hunter 2000, Bowne and Bowers 2004) and relatively small range of suitable habitat (Houlahan and Findlay 2003). Amphibian populations generally have a positive relationship with forest cover and a negative relationship with fragmented landscapes (Cushman 2005). Fragmentation reduces dispersal ability and increases patch isolation, decreasing genetic diversity and leaving populations vulnerable to extinction (Cushman 2005). A significant cause

of habitat fragmentation is roads, which can cause population declines due to road mortality, particularly for species with higher vagilities as they are more likely to come into contact with a road (Carr and Fahrig 2001).

In this thesis I am exploring the nighttime movement patterns and habitat use of two *Anaxyrus* species to develop a greater understanding of how these species interact with their habitat. In the first chapter I will present my research on the differences between the species' habitat use. In the second chapter I discuss my research on how environmental factors influence movement away from the roost site as well as general nighttime movement. My research looks at understudied topics that contribute to our general knowledge of these species that can be used in conservation planning.

Chapter 1- Nighttime Habitat Use of *Anaxyrus fowleri* and *Anaxyrus americanus*

Introduction

Wetlands are amongst the most threatened ecosystems in the United States with 53% of wetland habitat lost since 1780 (Belford 1999). Upland forest surrounding these bodies of water are also experiencing high levels of degradation (Noss et al. 1995), largely due to urban development. These forests serve as important buffers around breeding areas for amphibians as well as links between populations (Baldwin et al. 2006). The destruction of these habitats leave amphibians particularly vulnerable, due to their use of both aquatic and terrestrial ecosystems. In order to create best management practices to prevent further species extinctions, it is vital to precisely understand amphibian habitat use (Cushman 2005).

Various microhabitats and substrates have different temperature and moisture qualities, making this selection vital for the survival of amphibians as ectotherms vulnerable to desiccation (Bartelt et al. 2004). Many studies have examined habitat use throughout many species (Bartelt et al. 2004, Trenham and Shaffer 2005, Baldwin et al. 2006), with noteable gaps in our current knowledge. Prior habitat selection studies are often biased because they focus on roost sites. The majority of habitat use studies track individuals and locate them during the day. While these habitat selections are important, this does not include how species use their habitat to forage or breed, as amphibians are nocturnal. Additionally, an important factor influencing amphibian habitat selection is the threat of desiccation; however, water loss is generally less at night than during the day, so it would be likely that habitat use is different during the night than the day (Rittenhouse et al. 2008). Without tracking amphibians at night, a large portion of habitat use is

left out of consideration, which is particularly important when creating species management plans.

Nighttime habitat use has been investigated in previous studies, however, there are significant drawbacks to each one. Fritts et al. (2015) experimentally analyzed the microhabitat selection of *Anaxyrus terrestris* in the southeastern United States. In this study, they analyzed selection within four treatments of varying levels and spatial distributions of coarse woody debris. Despite the benefit of being experimental, this study limits the number of microhabitat choices and does not reflect the variety of microhabitats and substrates present in the natural habitat of *A. terrestris*. Graeter et al. (2008) analyzed nighttime movement of amphibians in the field, however, this was a very short term study. They tracked individuals using fluorescent powdered pigments, so the distance the individuals were followed was very limited. The only *Anaxyrus* species followed was *Anaxyrus terrestris*, which habitat use was only noted at 5m and at the endpoint, when the individual was either found or the powder was no longer detectable. At these locations Graeter et al. (2008) noted the substrate the individual was located on and if it was in a forest or in a clear cut area, which leaves out numerous other important environmental factors, such as the tree composition of the area. Beyond these studies, there is a little knowledge about nighttime habitat selection of amphibians.

In this study I analyzed the habitat use of two toad species, *A. fowleri* and *A. americanus*, in the southeastern United States for two months. On the habitat scale, I hypothesized that distance to the nearest permanent body of water would explain a difference between the two species due to their differences in breeding season. I hypothesized that the macrohabitat use of the two species would differ, with the density of large trees and coniferous trees explaining a difference between the two species. Due to the difference in their breeding season, I

hypothesized that the species would be located in different microhabitats and use different substrates as one species focuses on breeding and the other foraging.

Methods

Study Sites

My study was conducted at three sites within Williamsburg County and James City County, Virginia: College Woods of William & Mary (37° 16' 30.72"N -76° 43' 24.24"E), Warhill Sports Complex (37° 19' 26.4"N -76° 45' 37.08"E), and Greensprings Interpretive Trail (37° 14' 59.64"N -76° 47' 28.68"E). All sites contain some delineated wetlands. Greensprings and Warhill also contain human-made storm water retention ponds.

Species Selection

Two species were used in this study, the American Toad, *Anaxyrus americanus*, and the Fowler's Toad, *Anaxyrus fowleri.* I chose these species due to their sympatric use of forest land cover and availability at the study sites. Both species were present at two of the sites, Warhill and Greensprings, whereas only *A. americanus* was present at the College Woods.

A. fowleri have brownish grayish coloration. This species has more than three warts within the largest dark spot on its back. This morphologically differentiates it from *A. americanus* which have three or fewer (Savannah River Ecology Laboratory, accessed April 2019). *A. fowleri* occur throughout the eastern United States, excluding the Coastal Plain of South Carolina and Georgia and the majority of Florida, and southeastern Canada (Savannah River Ecology Laboratory, accessed April 2019). They often inhabit wooded areas near permanent sources of water (Virginia Herpetological Society). Their breeding season occurs from March to July (Virginia Herpetological Society).

At time of last consideration (2015) the IUCN considered *A. fowleri* a species of least concern. However, it is a federally protected species in Canada due to population declines (Tupper and Jones 2015). Despite *A. fowleri* receiving a global ranking of "secure," the Committee on the Status of Endangered Wildlife in Canada and the Ministry of Natural Resources and Forestry rank the species as "threatened" (Oldham 2003). The United States does not consider it to be a species of concern despite population decline (Adams et al. 2013, Walls et al. 2011, Jones and Tupper 2015, Vogel and Pechmann 2010). There has been an estimated 53% decrease in *A. fowerli* occupancy within Maryland and Virginia between 1999 and 2012 (Jones and Tupper 2015). These declines have numerous potential causes including competition with invasive species (Vogel and Pechmann 2010, Vogel and Johnson 2008), landscape changes, and anthropogenic effects, such as pesticide use and habitat degradation (Jones and Tupper 2015).

A. americanus are gray or brown with yellow or tan patches. This species is found in every southeastern state other than Florida and their range extends into the northeast to parts of Canada and west to eastern Kansas and the Dakotas. They are often found in wooded areas, as well as open and developed areas (Savannah River Ecology Laboratory, accessed April 2019). Their breeding season in the southeastern United States lasts from February to May (C. Check pers. comm.). Unlike many other amphibians, there has been no documentation of population declines for this species (Adams et al. 2013).

Tagging and Relocation

We caught 25 individuals between June and August 2018, 9 *A. americanus* individuals and 16 *A. fowleri* individuals. Any individuals that were not found after one to two days after their tagging were not included in this study. To catch individuals we went to the sites at night, particularly on rainy nights, and caught them by hand. Once a toad was captured we weighed it,

then tied a belt with a transponder (around 0.7 grams combined) directly above its hind legs around its waist. The belt was thin silicon tubing with a cotton thread inserted to tie it together around the waist. It was painted with unique color combinations in order to distinguish between individuals. The transponder was attached to the belt with non-toxic aquarium silicon and positioned along the anterior-posterior axis. The weight of the belt and transponder never exceeded 10% of the individual's mass and for the great majority it was less than 5%. The belts do not affect movement or habitat use (Rowley and Alford 2007) and no abrasions were detected on any individual. This research has been approved by College of William and Mary IACUC (Protocol IACUC-2017-02-20-11745-mleu).

Each site was visited approximately two times a week during the night and day, with one team of researchers visiting during the day and another at night. The individuals were located once during the day. At night, the individuals were located at least twice, unless the individual was unable to be relocated. If the individual was active during the first observation, I waited 20 minutes before relocating. In those situations, I relocated the individual a third time at least an hour after the second observation. Nights that an individual was inactive during the first observations, I waited approximately an hour before relocating. The toads were relocated using a device that uses acoustic telemetry (RECCO® Rescue System, Lidingö, Sweden). The device releases a microwave signal that reflects off of the transponder attached to the individual, back to the device as an acoustic signal. Each location where an individual was discovered was georeferenced using a GPS unit (Garmin GPSmap 62). We tracked individuals until the belt detached, the individual went missing, or was depredated. During every night visit I listened for calling of *A. fowleri* to determine status of breeding season. No *A. americanus* were ever documented calling as they were not in their breeding season.

Habitat Use

I investigated habitat use for the two species at four spatial extents: local, macrohabitat, microhabitat, and substrate. In this study, local extent represents the entire study area and macrohabitat is an area based on species-specific movement. Microhabitat is a 1 m^2 area, while substrate is the specific environmental feature on which the individual is sitting. I chose these extents on the basis of their life history and daily movement patterns.

Local Habitat

The forest habitat surrounding wetlands has been documented as critical for the success of non-breeding activities (Jones and Tupper et al. 2015). I predicted that *A. americanus* would be farther from bodies of water than *A. foweleri*, which was still breeding during this study. To calculate distance to water I used World Imagery base map provided in ArcMap 10.4 and digitized the permanent bodies of water present at each site. This provided a more precise delineation of the bodies of water than a water base layer. I then ran a Euclidean distance from the water within the extent of each study site.

Macrohabitat

Tree composition has been documented as an important factor in toad presence. Jones and Tupper (2015) found an association between decreased softwood forest habitat, which largely consists of coniferous trees, and decreased *A. fowleri* populations in Virginia and a negative correlation between *A. fowleri* occupancy and deciduous forest. *A. americanus* uses both deciduous and coniferous habitat (Boleck and Coggins 2003). I predicted that tree composition would explain a difference in habitat use between the two species, with *A. fowleri* using coniferous forests more. Based on field observations, I also predicted that both species

would use larger trees, as individuals used buttress roots as refuges. All sites were mixed habitats, including coniferous and deciduous trees. I estimated tree composition in a circular plot centered on each observation, with the radius representing the species average daily movement (*A. fowerli* = 12 m, *A. americanus* = 6 m; C. Check, unpubl. data). For each tree in the plot I recorded tree type (deciduous, coniferous, or snag) and diameter at breast height (DBH, approximately 1.3 m above ground). Snag is a dead tree that has not fallen over. If the distance between observations for an individual was less than half of the species-specific radius, we did not re-measure the tree composition or DBH. We did not measure individual DBH for trees with DBH < 5 cm. I calculated the number of coniferous, deciduous, snag, and total trees in different size guilds, based on the quantiles of tree size, (<5, 5-6, 6-8.8, 8.8-15, >15). Due to the difference in area measured for each species, tree density was calculated for each type and size guild, rather than total basal area.

Microhabitat

The microhabitat assemblages between all three sites were similar with each site containing bare ground, leaf litter, coarse woody debris (CWD, >5 cm in diameter), woody debris (<5 cm in diameter), herbaceous vegetation, moss, path, mowed grass, path (gravel or sand), and trees. Warhill and Greensprings also both have areas of mowed grass, more considerably at Warhill, while Matoaka does not. It has been often been reported that during the day toads use microhabitats with adequate coverage (Graeter et al. 2008); however, I predicted that at night the need to breed, move, and forage would cause both species to be present in more open areas. Consequently, I predicted that both species would be more present in bare ground or grassy areas (Eggert 2002, Hanlin 2000) and avoid overly vegetated areas at night (Eggert 2002). Fritts et al. (2015), experimentally demonstrated that at night, southern toads (*Anaxyrus*

terrestris) select against areas containing CWD, likely to forage. I predicted that both species would use areas without CWD to forage as well as to breed. I measured microhabitat by taking a picture of a 1 m^2 quadrat, centered on the observation point the morning after survey. I visually reviewed these photographs and determined the percentage of each microhabitat feature within each quadrat. I validated these estimates by uploading randomly chosen photographs into ArcMap, digitally tracing each feature, then calculating the proportion of each variable. Any feature present in fewer than 5% of observations was considered unimportant and excluded from analysis. This included: bridge, water, pipe, aquatic vegetation, and tree. Japanese stiltgrass (*Microstegium vimineum*) met this criterion was added to the herbaceous category.

Substrate

Substrate use is important for amphibians due to their need to thermoregulate and prevent water loss (Clark 1974). However, during the months of this study it seemed unlikely that these species would need to use substrate to warm themselves. In addition, toads often use CWD to prevent water loss, but water loss is a larger concern during the day than the night (Fritts et al. 2015). Therefore, I predicted that both species would use the top of leaf litter or grass more than CWD. The top of leaf litter and grass would allow individuals to forage and look for a mate. I classified 6 types of substrate, the structures on which the toads were located: CWD, mowed grass, buried under leaf litter, on top of leaf litter, path, and tree cavity. Bare ground, marsh, burrowed underground, and vegetation were all removed from analysis because they appeared in fewer than 10% of observations.

Statistical Analysis

To determine habitat use between species, I ran a logistic regression analysis with *A. fowerli* coded as 0 and *A. americanus* as 1. I centered and standardized all covariates centered (observation-mean/standard deviation) and calculated the Pearson's Correlation Coefficient between every variable to ensure that correlated variables (>0.7) were not included in the same models. I did not use mixed linear models because we lacked sufficient replication at the site level, the minimum of which is at least 5 levels (Bolker et al. 2009). To account for among site variation, I included sites as fixed effects. I analyzed linear, quadratic, and log forms of each covariate (Scherer et al. 2012) at each spatial scale (distance to water, tree density, microhabitat, and substrate). I chose the best variable per spatial scale, based on Akaike information criterion adjusted for small sample size, AICc, to use in the multivariable model. If variables were within two ΔAICc they were considered equal (Burnham and Anderson 2002) and were both brought into the multivariable model. Within the microhabitat analysis, the quadratic function of coarse woody debris was removed due to failure to converge.

Once the best covariate(s) per scale was determined, I included them in multivariable models (Table 1). I first included only larger scale variables, distance to water and tree density, then included combinations of microhabitat and substrate. I reported the models that had a cumulative AICc weight of approximately 0.95. I performed all statistical analyses were performed using R statistical software (R Core Team 2017).

Results

A. americanus had 141 observations and *A. fowerli* had 76 among the 25 individuals over the course of the two months. I went out four nights a week, generally between 8:30 pm and midnight. The most observations of an individual was 28 and the least was three. I had 47

observations of *A. americanus* at all three sites, then 39 observations of *A. fowerli* at Warhill and 25 at Greensprings.

The most important covariate from the habitat analysis was the quadratic form of distance to water. This association showed that *A. fowleri* used habitat closer to water than *A. amercanus.* The macrohabitat analysis showed that the density of deciduous trees >15 cm was the most important variable on this scale. Other tree types and size guilds carried 0 AICc weight. On the microhabitat scale, leaf litter had the largest effect. However, mowed grass and the psuedothreshold form of bare ground were within two ΔAICc, so they were included in the multivariable analysis considered to be equally important as grass. These covariates were brought into the multivariable analysis. All AICc values for the univariate analyses are reported in Appendix 1.

The top multivariable model included the quadratic form of distance to water, the density of deciduous trees with DBH >15 cm, mowed grass, and grass substrate (Table 1). This was the strongest model with an AICc weight of 0.74. The second best model included all of the top covariates from the univariate analysis: quadratic form of distance to water, the density of deciduous trees with DBH >15 cm, leaf litter, the psuedothreshold form of bare ground, and grass substrate. This model had an AICc weight of 0.13. The next multivariable model resulted in a cumulative AICc weight of 0.95, with an individual AICc weight of 0.08. This model included the quadratic form of distance to water, the density of deciduous trees with a DBH >15 cm, the psuedothreshold form of bare ground, and grass substrate.

Table 1: The top three multivariable model explaining species habitat use based on AICc analysis. Models were built on the basis of logistic regression analysis. For each model I report: K= number of parameters, AICcWt = AICc weight per model, Cum.Wt = cumulative weight of the models, LL= log likelihood. For reference, I added the null model.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Distance to Water (Quadratic) + Deciduous >15 cm + Mowed Grass + Grass	8	102.73	0	0.74	0.74	-43.00
Distance to Water (Quadratic) + Deciduous >15 cm + Leaf Litter + Mowed Grass + Bare Ground (Threshold) + Grass	10	106.13	3.4	0.13	0.87	-42.49
Distance to Water (Quadratic) + Deciduous >15 cm + Bare Ground (Threshold) + Grass . . .	8	107.09	4.36	0.080	0.95	-45.17
Null	1	283.07	180.34	0	1	-140.53

On the basis of the values given to each species (*A. fowleri* = 0, *A. americanus* = 1), variables with negative effect size better explain *A. fowerli* use, while positive explain *A. americanus* use. Based on the model average from the top three multivariable models, the distance to water was the most important variable. The quadratic relationship indicates that *A. fowerli* used habitat closer to water, and *A. americanus* used habitat farther away from water, up to a certain distance. Density of deciduous trees with DBH >15 cm was the second best explanatory variable, *A. americanus* used areas with greater densities of deciduous trees with DBH >15 cm more than *A. fowleri.* The confidence interval of the remaining variables all crossed 0, indicating that leaf litter, mowed grass, and grass as a substrate explained both species' habitat use.

Table 2: The weighted average of the variables from the top three models. SE represents the standard error.

Model	Effect Size	Standard Error	Weight
DH2O	2.40	0.52	0.95
DH2O(Quad)	1.57	0.54	0.95
Deciduous >15	0.90	0.37	0.95
Grass	0.24	0.30	0.95
Bare Ground	0.015	0.014	0.21
Leaf Litter	-0.012	0.037	0.13
Grassy Patch	-2.33	2.29	0.87

Discussion

My results show the similarities and differences between *A. fowerli* and *A. americanus* habitat use at night. On a larger scale, the species show differences in how they use habitat in proximity to water. My data suggest that *A. americanus* is farther away from water in the summer months than *A. fowerli*. In addition, *A. americanus* is found in areas of higher density of deciduous trees >15 cm DBH. There are more similarities between the two species at the microhabitat scale. Bare ground, leaf litter, and mowed grass are all important explanatory variables for both species' habitat use, with grass the most used substrate for both species.

Habitat

My results reflected expected habitat use differences between the species due to differences in breeding season. *A. fowerli* were actively breeding so they were closer to water, which has been demonstrated in numerous other studies (Dodd 1996, Ficetola and Bernardi

2004). The shortest distance to water was from an *A. fowerli* observation and was approximately 4 m. The greatest distance was from an *A. americanus* observation and was approximately 112 m. The use of habitat farther away from bodies of water by *A. americanus* demonstrates the importance of upland habitat after the breeding season.

Macrohabitat

The use of large deciduous trees by *A. americanus* is likely due to the presence of buttress roots in larger deciduous trees. These roots provide refugia from predation and protection from high temperatures that are associated with desiccation. Although deciduous trees dominated the forest in all sites, the density of large deciduous trees was important, rather than the density of total large trees. This indicates that *A. americanus* are using deciduous trees. However, trees were only important within the macrohabitat (defined at 113 m^2 for *A. americanus*). Presence of trees in the microhabitat and trees as a substrate were both removed from analysis due to the fact that they appeared in less than 10% of observations, indicating that while *A. americanus* were in areas of large trees at night, they were not using them. This is likely due to the fact that toads forage at night. Tree density was likely not an important variable for *A. fowerli* habitat use because they moved greater distances away from their roost site (see Chapter 2), allowing them to get farther away from the high density of forest. There is a larger spatial separation between roost site and foraging area for *A. fowerli* than *A. americanus*, with *A. americanus* staying closer to the forest (DeGraaf and Rudis 1990).

Microhabitat and Substrate

My results show a large overlap of microhabitat and substrate use between the two species. Despite their difference in life stage during the summer, foraging versus breeding, both

species used open areas. This demonstrates the difference in habitat use between night and day, as amphibians use leaf litter and coarse woody debris to prevent predation or desiccation during the day (Rittenhouse et al. 2008). Although leaf litter was used frequently on the microhabitat scale, leaf litter was not an important substrate for either species. They were not buried in leaf litter, which is how they use it during the day, nor were they on top of it. During the day, both species also use coarse woody debris, which was not an important variable at night for microhabitat or substrate use (Graeter et al. 2008). The sympatric use of open habitat may also point to the importance of visibility when foraging. *A. fowerli* have been previously shown to be visual foragers, and therefore rely on open areas such as bare ground and mowed grass (Clarke 1974), but this has not been shown in *A. americanus.* Due to both species' use of open areas and the extensive network of paths throughout all study sites, I expected paths to be an important microhabitat and substrate, as these paths provide similar levels of camouflage, visibility, and heat as bare ground. However, paths were not an important variable for either species. Although paths provide a similar microhabitat or substrate as bare ground in forests, I hypothesized that these two species do not use paths because they are unnatural. The artificial nature and frequency of human interference on these paths, although they are relatively undisturbed at night, may prevent these species from using this habitat. Although *A. fowerli* were not expected to use paths as they are not associated with developed areas, *A. americanus* have been documented to also occur in more urban areas, and therefore I would have expected them to use paths. This contradictory result needs further investigation.

My results demonstrate that *A. fowerli* and *A. americanus* use their habitats differently at night than during the day. This is an important consideration when creating conservation plans. Many states have buffer zone regulations around bodies of water (National Academy Press 2002)

that typically range from 15 m (Baird & Wetmore 2004) to 31 m (Goates et al. 2007). Buffer zones are delineated to protect these habitats from human activity, however, they are often created to protect water quality rather than biodiversity (Goates et al. 2007). Therefore, the habitat inside the buffer zone is not critically assessed. Based on my results, these species need open spaces in order to forage and breed, so a buffer zone of only dense forest would not be beneficial. This demonstrates that it is crucial to understand the complexities of how species use their habitat, including their nighttime use.

The similarities between the two species' habitat use raises an important question of why these species' populations are faring so differently. With the *A. fowerli* showing declining populations and *A. americanus* remaining stable (Adams et al. 2013), I would have expected to find different use of habitat between the species. This study was conducted in the middle of these species ranges, so it is possible their habitat use may be different on the edges of their ranges, where *A. fowerli* is experiencing population declines (Tupper and Jones 2015). This question requires further research.

Chapter 2- Nighttime Movement of *A. fowerli and A. americanus*

Introduction

In past decades, research on amphibians was largely limited to aquatic studies on the larval stage (Pittman et al. 2014). This focus was due to the difficulty of tracking amphibians on land due to their cryptic nature and small size. However, updated technology, such as harmonic direction finding, has made it easier to track terrestrial movements of amphibians (Alford and Rowley 2007). This has been very beneficial because individual movement studies can be useful in conservation due to the potential to extrapolate to the population level (Fritts et al. 2015).

Most movement studies often do not analyze fine scale movement (Eggert 2002) and focus on larger scale movements, such as movement away from the breeding pond (Eggbert 2002, Tatarian 2008). These studies often only locate individuals every few days (Bartelt et al. 2004). Despite being understudied, an animal's hourly movements are important as they result in home ranges and dispersal patterns (Marchand et al. 2017). Movement studies have also generally not collected data frequently enough to detect foraging behavior. Amphibians may have many tortuous movements when foraging, but have a very small net displacement (Pittman et al. 2014). By focusing solely on displacement, the full extent of their movement is not being captured. This study analyzes the displacement from the diurnal roost site, as well as smaller, hourly movements in order to provide a better understanding of the complex ways these species interact with their environment.

Methods

For site and species selection and tagging methods see Chapter 1.

Movement

Every georeferenced observation was uploaded to ESRI's ArcMap 10.4 projected into NAD 1983 UTM Zone 18N (ESRI, Redlands CA). Distances were measured in ArcMap. The greatest distance between observations in a given night was used as the within night movement per individual. The greatest distance between a night point and a roost site were used as the distance from roost site per individual. The roost site was considered the most recent record of day location of the individual, either before or after the night observation.

Rain

Rain was associated with movement and migrations across many species, including those that are predominantly terrestrial. However, higher amounts of daily rain have also been correlated with increased daily movement (Fellers and Kleeman 2007, Todd and Winne 2006). I predicted that although the species are at different stages of their breeding seasons, both species will increase movement during times of increased rain (Vasconcelos and Calhoun 2004, Todd and Winne 2006). All weather data were gathered from Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2018). Latitude and longitude were used to retrieve weather information from each site. The daily total precipitation were collected from PRISM for the day of and the seven days before night observation. These values were then averaged to get the average rainfall of the week. The precipitation for the day of observation, the prior day, and the week average were considered in analyses. The daily precipitation was used to determine the number of days since rain. Average rainfall was calculated based on every day over the study period at each study site. Days that had average or above average rainfall were given a value of 1, and days with less than average rainfall were given a value of 0. Days since above average rain were based on these values.

Temperature

Because amphibians are ectotherms, it is likely that weather directly affects their activity, particularly temperature (Sexton et al 1990). This connection has been confirmed by numerous studies that indicate that increased temperature results in increased activity (Mazerolle 2001, Vasconcelos and Calhoun 2004, Bartlet et al. 2004) and migration (Timm et al. 2007). Due to increased activity, I predicted that temperature would be non-linearly related to movement, with increased temperature, up to a certain degree, explaining increased movement from the roost site and general nighttime movement for both species. As too-high temperatures could leave the toads vulnerable to desiccation. I used the same methods to gather minimum, maximum, and mean temperature data as I did for rain data.

Humidity

Higher humidity helps reduce water loss and allows for amphibians to spend less time on substrate that protects against desiccation (Campbell and Norman 1998). Previous studies have found associations between higher humidity and greater lengths of nighttime movement of toads (Bartelt et al. 2004, Campbell and Normal 1998). This is likely due to the decreased threat of desiccation. I predicted that increased humidity would result in increased movement from the roost site and general nighttime movement for both species. I calculated relative humidity using temperature and temperature at dew point, both collected from PRISM.

Statistical Analysis

Distance from roost site and distance between night points were used as response variables in two separate analyses. The total number of observations was 219. Due to the non-normal distribution and overdispersal of the response variables, I created negative binomial generalized linear models using the lme4 package in R statistical software (R Core Team 2017). I

included species as a covariate, where *A. fowerli* was given a value of 0 and *A . americanus* a value of 1. All other covariates were centered and standardized (observation-mean/standard deviation). I did not include site as a random factor because I only had three levels (number of sites) and five levels are required for a linear mixed model (Bolker et al. 2009). To account for this and the variability among sites, I included sites as fixed effects. Linear, quadratic, and psuedothreshold forms of each covariate were considered (Scherer et al. 2012), as well as the interaction between Julian date and species for all covariates

I chose the best variable form or interaction for each weather metric (temperature, rain, humidity, and seasonal average rain) to bring into the multivariable models on the basis Akaike information criterion adjusted for small sample size, AICc. If variables were within two ΔAICc, they were considered equal (Burnam and Anderson 2002) and were both brought into the multivariable model. All covariates were checked for multicollinearity using Pearson's correlation coefficient, and if two variables were highly correlated (>0.7) they were not include in the same models. Once the best covariate(s) per metric was determined, I included them in multivariable models. I reported the models that had a cumulative AICc weight of approximately 0.95.

Results

Between June 6th and August 1st 2018, I collected 141 observations of *A. americanus* and 78 of *A. fowerli*. Across both species, the average distance moved from the roost site was 15 m, with a standard error of 1.17, and the average distance moved between night observations was 8 m, with a standard error of 0.99. These distinct distance measurements were not correlated (r = 0.43). Roost site observation and nightly observation were most often on the same day with 68%

of observations happening on the same day, 20% with one day in between, and 10% with two days in between.

Distance from Roost Site

The most important covariate from the candidate set of temperature variables was the interaction between Julian date and the minimum temperature of the day of observation. However, the interaction between Julian date and average minimum temperature of the week was within two ΔAICc, so they were considered equally important. No form or measurement of maximum or mean temperature were important explanatory variables. The interaction between Julian date and the average weekly rain explained the most variation in movement from the rain candidate set. No forms of rain the day of observation or the day before were important to explain variation in distance moved. I analyzed days since rain, days since above average rain, and average rain separately from the other rain variables as they were based on seasonal averages rather than weekly. Of these, days since above average rain was the only the only important variable. The most important covariate from the humidity analysis was the interaction between Julian date and humidity of the day of observation. However, the interaction between Julian date and average weekly humidity was within two ΔAICc of the top humidity variable so it was considered equally important (Burnham and Anderson 2002). These top variables from the scaled analysis were used in multivariable models. All AICc values for the univariate analyses are reported in Appendix 2.

Table 1: Top two multivariable models explaining distance moved from roost site based on AICc analysis. Models were built on the basis on negative binomial generalized linear model. Sites and species were included in all models but were not shown in this table. For each model I report: K= number of parameters, AICcWt = AICc weight per model, Cum.Wt = cumulative weight of the models, LL= log likelihood. For reference, I added the null model.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Julian Date* Weekly Average Humidity + Julian Date*Weekly Average Rain + Julian Date*Weekly Average Minimum Temperature	12	1617.11	0	0.9	0.9	-795.86
Julian Date* Weekly Average Minimum Temperature + Days Since Above Average Rain	9	1622.36	5.24	0.07	0.97	-801.78
. . .						
Null	2	1684.75	67.63	0	1	-840.35

The top multivariable model included the interaction between Julian date and average daily minimum temperature, the interaction between Julian date and average daily rain, and the interaction between Julian date and average daily humidity (Table 1). This was the strongest model with the AICc weight of 0.9. The second best multivariable model included the interaction between Julian date and average daily minimum temperature and days since above average rain, but this model only had an AICc weight of 0.07. The interaction between Julian date and daily minimum temperature and Julian date and daily humidity were both included in the multivariable analysis, but were not a part of the top models.

Based on the model average from the top two multivariable models, the weekly average minimum temperature was the best predictor of a greater distance moved, with higher minimum

temperatures explaining greater distances (Table 2). Average daily rain was the second best predictor and had a similar effect size and the same directionality as weekly average minimum temperature. Additionally, the fewer days since above average rain, the greater the movement from roost site. Julian date negatively related to movement. The negative estimate of species shows that *A. fowleri* moved greater distances than *A. americanus*. On average, *A. fowerli* moved 23 m from the roost site, with a standard error of 1.98, and *A. americanus* moved 10 m, with a standard error of 1.45. Although included in the top models, the interaction between Julian date and weekly average rain, Julian date and weekly average humidity, and average daily humidity were all weak predictors as the confidence interval of their effect sizes crossed zero.

Table 2: The weight, average estimate, and average standard error of the covariates included in the final models. Sites were included in the final models but are not included in this table as they are not a variable of interest in this study. The standard error is reported.

Model	Effect Size	Standard Error	Weight
Weekly Average Minimum Temperature	0.47	0.11	0.97
Weekly Average Rain	0.46	0.23	0.9
Julian Date*Weekly Average Minimum Temperature	0.39	0.12	0.97
Julian Date*Weekly Average Rain	0.0086	0.20	0.9
Days Since Above Average Rain	-0.016	0.0061	0.07
Weekly Average Humidity	-0.031	0.13	0.9
Julian Date*Weekly Average Humidity	-0.15	0.098	0.9
Julian Date	-0.40	0.10	0.97
Species	-0.92	0.18	0.97

Distance between Night Observations

The most important covariate from the candidate set of temperature variables was the quadratic form of the minimum temperature on the day of observation. Similarly to the distance

moved from the roost site, no form or measurement of maximum or mean temperature were important explanatory variables. Average weekly rain explained the most variation in movement from the rain candidate set. No forms of rain the day of observation or the day before were important to distance moved. Unlike for the distance moved from roost site, the interaction of rain with Julian date was not important. However, days since above average rain was an important explanatory variable for distance between night observations, as well as from roost site. The most important humidity covariate was the psuedothreshold form on the day of observation. However, the interaction between Julian date and humidity the day before was within two ΔAICc of the top humidity variable, so it was considered equally important (Burnham and Anderson 2002). These top variables were carried forward to the multivariable models. All AICc values for the univariate analyses are reported in Appendix 3.

The top multivariable model included days since above average rain, the quadratic form of minimum temperature, and the psuedothreshold form of humidity (Table 3). The second best multivariable model included the days since above average rain and quadratic form of minimum temperature. The interaction between Julian date and the quadratic form of the humidity of the day before and weekly average rain were both included in the multivariable analysis, but were not a part of the top models.

Table 3: Top two multivariable models explaining nighttime movement based on AICc analysis. Models were built on the basis on negative binomial generalized linear model. Sites and species were included in all models but were not shown in this table. For each model I report: K= number of parameters, AICcWt = AICc weight per model, Cum.Wt = cumulative weight of the models, LL= log likelihood. For reference, I added the null model.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Days Since Above Average Rain + Minimum Temperature (Quadratic) + Humidity (Threshold)	9	822.99	0	0.69	0.69	-402.0
Minimum Temperature (Quadratic) + Days Since Above Average Rain	8	824.6	1.61	0.31	1	-403.91
. . .						
Null	2	889.06	66.07	0	1	-442.5

Based on the model average from the top two multivariable models, the psuedothreshold of humidity was the best predictor of a greater distance moved, with higher humidity associated with larger distances moved (Table 4). Minimum temperature was the second best explanatory variable, with the toads moving greater distances with higher minimum temperatures. Additionally, the fewer days since above average rain, the greater the movement. The negative estimate of species again shows that *A. fowleri* move greater distances than *A. americanus*. The average between night observations was 3 m for *A. americanus,* with a standard error of 1.23, and 17 m for *A. fowerli,* with a standard error of 1.69.

Table 4: The weight, average estimate, and average standard error of the covariates included in the final models. Sites were included in the final models but are not included in this table as they are not a variable of interest in this study. The standard error is reported.

Model	Effect Size	Standard Error	Weight
Humidity (Threshold)	1.82	0.87	0.69
Minimum Temperature	1.18	0.34	1
Days Since Above Average Rain	-0.82	0.21	1
Minimum Temperature (Quadratic)	-1.27	0.4	1
Species	-2.56	0.39	1

Discussion

To my knowledge, this is the first research that looked into how variability in weather affects movement from roost sites and nightly movements on such a fine scale. My results show that these species are making smaller movements at night that are not captured by studies looking at movement between days or multiple days. *A. fowerli* are making larger movements from the roost site and between night observations than *A. americanus.* The movements of both species are associated with weather variables, with increased rain, humidity, and minimum temperature explaining greater nighttime movements. In addition, movement from roost site is negatively associated with Julian date, as movements shorten as the summer goes on.

While weather factors are important to explain nighttime movement, there are important differences between movement from the roost site and between nighttime observations. I measured the distance from roost site in order to capture how far these species are leaving their diurnal refuge to breed and forage, and distance between night observations to show smaller movements. It seems likely that the farther an individual moves from a roost site the less likely they are to return to the same location, and will find a new roost site. These distances were

impacted by weekly averages of rain and minimum temperature. Previous studies have demonstrated that longer term weather patterns lead to larger movements, such as migration (Eggert 2002, Tatarian 2008). It appears that weather variables must be relatively consistent, average high temperature, humidity, and rainfall, in order for these species to move to a new roost site. I hypothesize that these species relocate to new roost sites in optimal weather conditions, associated with a weather envelope where a certain range of temperature and precipitation are needed for greater movements. However, distance between night observations, which was not correlated with distance from roost site, is likely more for the purpose of foraging or breeding, rather than moving to a new refuge. These movements are smaller and are explained by daily minimum temperature and humidity. However, both types of movement were negatively associated with days since above average rain, indicating that large rain events are important for overall movement. Similarly, the association between above average rain and migration (Fellers and Kleeman 2007) clearly supporting the notion that large rain events are important to amphibian ecology.

Although *A. Fowerli* moved greater distances for both measurements, Julian date was an important explanatory variable for decreasing distance from roost site. As the breeding season goes on, *A. fowerli* were making smaller movements away from their roost site. This is consistent with previous studies' findings that species move greater during the breeding season (Tatarian 2008). However, Julian date was not important for distance moved between night observations, which demonstrates that both species make consistent small movements at night throughout the summer. These results provide more insight as to how these species spatially and temporally interact with their environment.

In future studies it would be beneficial to locate individuals the day before and after night observation. This would give a greater understanding of if the individual was returning to its roost site or moving to a new one. This would add clarity to the results, but was not possible for this study. Understanding night activity is vital in order to understand where these species forage and breed. Without studying these nighttime movements, a large part of their behavior is left out of analysis.

Appendix 1

Table 1: Forms of distance to water.

Distance **to Water**						
	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Distance to Water (Quadratic)	5	136.73	0	0.99	0.99	-63.22
Distance to Water	4	146.36	9.63	0.01	1	-69.09
Distance to Water (Pseudothreshold)	4	158.71	21.99	0	1	-75.26
Sites	3	225.56	88.83	0	1	-109.72
Null	1	283.07	146.35	0	1	-140.53

Table 2: Forms of tree composition.

Trees						
	K	AICc	Delta_AICc	CICcWt	Cum.Wt	LL
Deciduous >15	4	161.9	0	0.64	0.64	-76.86
Deciduous >15 (Quadratic)	5	163.05	1.14	0.36	1	-76.38

Total 6-8.8	4	180.93	19.03	0	1	-86.37
Total 6-8.8 (Quadratic)	4	180.93	19.03	0	1	-86.37
Deciduous >15 (Threshold)	4	183.21	21.31	0	1	-87.51
Deciduous 6-8.8	4	189.44	27.53	0	1	-90.62
Deciduous 6-8.8 (Quadratic)	5	191.53	29.63	0	1	-90.62
Deciduous 8.8-15 (Threshold)	4	194.16	32.26	0	1	-92.99
Coniferous >15 (Quadratic)	5	195.34	33.44	0	1	-92.53
Total >15	4	195.49	33.59	0	1	-93.65
Coniferous >15	4	195.5	33.59	0	1	-93.65
Deciduous 8.8-15	4	195.54	33.63	0	1	-93.67
Total >15 (Quadratic)	5	195.95	34.05	0	1	-92.83
Deciduous 8.8-15 (Quadratic)	5	196.51	34.61	0	1	-93.11
Coniferous >15 (Threshold)	4	196.62	34.71	0	1	-94.21
Snag 6-8.8 (Quadratic)	5	196.92	35.02	0	1	-93.32
Snag >15 (Quadratic)	5	197.56	35.66	0	1	-93.64

Total 8.8-15 (Threshold)	4	198.14	36.23	0	1	-94.97
Total 8.8-15	4	198.57	36.66	0	1	-95.19
Total 8.8-15 (Quadratic)	5	200.58	38.67	0	1	-95.15
Total 6-8.8 (Threshold)	4	203.47	41.56	0	1	-97.64
Total >15 (Threshold)	4	206.4	44.5	0	1	-99.11
Deciduous 6-8.8 (Threshold)	4	207.34	45.43	0	1	-99.58
Snag 6-8.8	4	207.69	45.79	0	1	-99.75
Deciduous 5-6	4	208.27	46.37	0	1	-100.04
Total 5-6	4	212.16	50.26	0	1	-101.99
Snag 6-8.8 (Threshold)	4	213.65	51.75	0	1	-102.73
Coniferous 5-6 (Threshold)	4	213.68	51.78	0	1	-102.75
Coniferous 6-8.8	4	213.98	52.08	0	1	-102.9
Snag <5	4	217.06	55.16	0	1	-104.44
Snag <5 (Quadratic)	5	217.94	56.03	0	1	-103.83
Coniferous 6-8.8 (Threshold)	4	218.53	56.63	0	1	-105.17
Coniferous <5 (Threshold)	4	218.68	56.78	0	1	-105.25

Deciduous <5 (Threshold)	4	219.47	57.57	0	1	-105.64
Total <5 (Threshold)	4	219.61	57.7	0	1	-105.71
Coniferous 8.8-15	4	221.04	59.14	0	1	-106.43
Total <5	4	221.51	59.61	0	1	-106.66
Deciduous <5	4	222.06	60.16	0	1	-106.94
No Trees	4	222.26	60.36	0	1	-107.04
No Trees (Quadratic)	4	222.26	60.36	0	1	-107.04
No Tree (Threshold)	4	222.26	60.36	0	1	-107.04
Coniferous 8.8-15 (Threshold)	4	222.89	60.99	0	1	-107.35
Snag 5-6 (Threshold)	4	223.4	61.49	0	1	-107.6
Total <5 (Quadratic)	5	223.61	61.7	0	1	-106.66
Snag <5 (Threshold)	4	223.91	62.01	0	1	-107.86
Deciduous <5 (Quadratic)	5	224.15	62.25	0	1	-106.93
Snag >15	4	225.33	63.43	0	1	-108.57
Sites	3	225.56	63.65	0	1	-109.72
Snag 8.8-15 (Threshold)	4	226.03	64.13	0	1	-108.92
Deciduous 5-6 (Threshold)	4	226.08	64.17	0	1	-108.94

Coniferous 5-6	4	226.5	64.59	0	1	-109.16
Total 5-6 (Threshold)	4	226.88	64.98	0	1	-109.35
Coniferous <5	4	227.25	65.35	0	1	-109.53
Snag 8.8-15	4	227.25	65.34	0	1	-109.53
Snag 5-6	4	227.41	65.5	0	1	-109.61
Snag >15 (Threshold)	4	227.47	65.57	0	1	-109.64
Null	1	283.07	121.17	0	1	-140.53

Table 3: Forms of microhabitat.

Microhabitat						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Leaf Litter	4	212.54	0	0.2	0.2	-102.17
Grassy Patch	4	212.68	0.14	0.19	0.39	-102.25
Grassy Patch (Threshold)	4	213.14	0.6	0.15	0.53	-102.48
Leaf Litter (Quadratic)	5	213.25	0.71	0.14	0.67	-101.48
Bare Ground (Threshold)	4	213.33	0.79	0.13	0.81	-102.57
Bare Ground (Quadratic)	5	213.95	1.41	0.1	0.91	-101.83
Grassy Patch (Quadratic)	5	214.77	2.24	0.07	0.97	-102.25
Leaf Litter (Threshold)	4	217.7	5.16	0.02	0.99	-104.75

Path (Quadratic)	4	220.22	7.68	0	0.99	-106.02
Path	4	220.47	7.93	0	1	-106.14
Coarse Woody Debris	4	223.44	10.9	0	1	-107.62
Moss (Quadratic)	5	223.9	11.36	0	1	-106.81
Path (Threshold)	4	224.19	11.65	0	1	-108
Site	3	225.56	13.02	0	1	-109.72
Coarse Woody Debris (Threshold)	4	225.81	13.27	0	1	-108.81
Moss	4	226.59	14.05	0	1	-109.2
Moss (Threshold)	4	226.72	14.19	0	1	-109.27
Herbaceous	4	226.83	14.29	0	1	-109.32
Herbaceous (Threshold)	4	227.07	14.53	0	1	-109.44
Bare Ground	4	227.6	15.06	0	1	-109.71
Herbaceous (Quadratic)	5	228.72	16.18	0	1	-109.22
Null	1	283.07	70.53	0	1	-140.53
Herbaceous (Quadratic)	5	228.72	16.18	0	1	-109.22
Null	1	283.07	70.53	0	1	-140.53

Table 4: Form of substrate.

Substrate	K	AICc	Delta_AICc	CICcWt	Cum.Wt	LL
Grass	4	195.88	0	0.33	0.33	-93.84
Grass (Quadratic)	4	195.88	0	0.33	0.66	-93.84
Grass (Threshold)	4	195.88	0	0.33	0.99	-93.84
Path (Quadratic)	5	205.98	10.1	0	0.99	-97.84
Leaf Litter Buried	4	206.2	10.32	0	0.99	-99
Leaf Litter Buried (Quadratic)	4	206.2	10.32	0	1	-99
Leaf Litter Buried (Threshold)	4	206.2	10.32	0	1	-99
Path	4	207.33	11.45	0	1	-99.57
Path (Threshold)	4	207.33	11.45	0	1	-99.57
Leaf Litter Top	4	210.25	14.37	0	1	-101.02
Leaf Litter Top (Quadratic)	4	210.25	14.37	0	1	-101.02
Leaf Litter Top (Threshold)	4	210.25	14.37	0	1	-101.02

Sites	3	225.56	29.68	0	1	-109.72
Null	1	283.07	87.19	0	1	-140.53

Table 5: All multivariable models.

	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Distance to Water (Quadratic)+Deciduous >15+Grassy Patch+ Grass	8	102.73	0	0.74	0.74	-43
Distance to Water (Quadratic)+Deciduous >15+Leaf Litter+Grassy Patch+Bare Ground (Threshold)+ Grass	10	106.13	3.4	0.13	0.87	-42.49
Distance to Water (Quadratic)+Deciduous >15+Bare Ground (Threshold)+ Grass	8	107.09	4.36	0.08	0.95	-45.17
Distance to Water (Quadratic)+Deciduous >15+Leaf Litter+ Grass	8	108.35	5.61	0.04	1	-45.8
Distance to Water (Quadratic)+Deciduous >15	6	115.06	12.32	0	1	-51.33
Sites	3	225.56	122.82	0	1	-109.72
Null	1	283.07	180.34	0	1	-140.53

Appendix 2

Temperature

	K	AICc	DeltaAICc	AICcWt	Cum.Wt	LL
Julian*Min Temp	9	1627.21	0	0.26	0.26	-804.21
Julian*Min Temp (Threshold)	9	1627.22	0	0.26	0.52	-804.21
Julian*Min Temp Avg (Quadratic)	10	1628.86	1.65	0.11	0.63	-803.94
Julian*Min Temp Avg (Threshold)	8	1629.55	2.34	0.08	0.71	-806.46
Julian*Min Temp 1 (Threshold)	8	1629.82	2.61	0.07	0.78	-806.6
Julian*Min Temp 1	8	1629.86	2.65	0.07	0.85	-806.61
Julian*Min Temp Avg	8	1630.01	2.8	0.06	0.92	-806.69
Julian*Min Temp (Quadratic)	11	1630.14	2.93	0.06	0.98	-803.48
Julian*Min Temp 1 (Quadratic)	10	1632.78	5.57	0.02	0.99	-805.91
Julian*Max Temp Avg (Threshold)	8	1637.7	10.49	0	1	-810.53
Julian*Max Temp Avg	8	1637.85	10.64	0	1	-810.61
Mean Temp Avg (Quadratic)	7	1638.67	11.45	0	1	-812.09
Julian*Max Temp (Threshold)	8	1639.75	12.54	0	1	-811.56
Julian*Max Temp	8	1639.82	12.6	0	1	-811.59

Julian (Quadratic)	7	1640.84	13.63	0	1	-813.18
Julian (Threshold)	6	1641.17	13.96	0	1	-814.4
Julian*Max Temp Avg (Quadratic)	10	1641.39	14.18	0	1	-810.21
Julian	6	1641.59	14.38	0	1	-814.61
Julian* Mean Temp Avg (Quadratic)	10	1641.62	14.4	0	1	-810.32
Julian*Max Temp (Quadratic)	10	1642.43	15.22	0	1	-810.73
Julian*Mean Temp 1 (Quadratic)	10	1644.1	16.89	0	1	-811.56
Julian*Mean Temp 1 (Threshold)	8	1644.18	16.96	0	1	-813.77
Julian*Max Temp 1 (Threshold)	8	1644.32	17.11	0	1	-813.85
Julian*Max Temp 1	8	1644.56	17.35	0	1	-813.97
Julian*Mean Temp 1	8	1644.65	17.44	0	1	-814.01
Julian* Mean Temp Avg (Threshold)	8	1645.22	18.01	0	1	-814.29
Julian*Mean Temp (Threshold)	8	1645.35	18.14	0	1	-814.36
Julian*Mean Temp	8	1645.73	18.52	0	1	-814.55
Julian* Mean Temp Avg	8	1645.74	18.52	0	1	-814.55
Julian*Mean Temp (Quadratic)	10	1646.04	18.83	0	1	-812.53
Julian*Max Temp 1 (Quadratic)	10	1646.54	19.33	0	1	-812.78
Max Temp (Quadratic)	7	1646.71	19.5	0	1	-816.11
Min Temp (Quadratic)	7	1648.83	21.62	0	1	-817.17
Max Temp Avg	6	1650.02	22.81	0	1	-818.83
Min Temp 1 (Threshold)	6	1650.03	22.82	0	1	-818.83
Max Temp Avg (Threshold)	6	1650.03	22.82	0	1	-818.83
Min Temp 1	6	1650.15	22.94	0	1	-818.89
Max Temp Avg (Quadratic)	7	1650.29	23.08	0	1	-817.9

Max Temp 1 (Quadratic)	7	1650.43	23.22	0	1	-817.97
Sites+Species	5	1650.82	23.61	0	1	-820.28
Mean Temp Avg (Threshold)	6	1650.88	23.67	0	1	-819.26
Max Temp 1 (Threshold)	6	1650.88	23.67	0	1	-819.26
Mean Temp Avg	6	1651.26	24.05	0	1	-819.45
Max Temp 1	6	1651.28	24.07	0	1	-819.46
Min Temp 1 (Quadratic)	7	1651.39	24.18	0	1	-818.45
Min Temp (Threshold)	6	1651.49	24.28	0	1	-819.56
Min Temp	6	1651.71	24.5	0	1	-819.67
Min Temp Avg (Threshold)	6	1652.12	24.9	0	1	-819.88
Min Temp Avg	6	1652.14	24.93	0	1	-819.89
Mean Temp	6	1652.66	25.45	0	1	-820.15
Mean Temp (Threshold)	6	1652.69	25.48	0	1	-820.16
Max Temp (Threshold)	6	1652.69	25.48	0	1	-820.16
Max Temp	6	1652.81	25.6	0	1	-820.22
Mean Temp 1	6	1652.91	25.7	0	1	-820.27
Mean Temp 1 (Threshold)	6	1652.92	25.71	0	1	-820.28
Mean Temp (Quadratic)	7	1653.92	26.71	0	1	-819.72
Min Temp Avg (Quadratic)	7	1654.2	26.99	0	1	-819.86
Mean Temp 1 (Quadratic)	7	1654.81	27.6	0	1	-820.16
Sites	4	1669.26	42.05	0	1	-830.54
Null	2	1684.75	57.53	0	1	-840.35

Table 2: Forms and measurements of rain.

Rain						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Julian*Rain Avg	8	1629.3	0	0.48	0.48	-806.33
Julian*Rain Avg (Threshold)	8	1629.5	0.21	0.43	0.92	-806.43
Julian*Rain Avg (Quadratic)	10	1633.01	3.71	0.08	0.99	-806.02
Julian (Quadratic)	7	1640.84	11.55	0	0.99	-813.18
Julian (Threshold)	6	1641.17	11.87	0	0.99	-814.4
Rain Avg (Threshold)	6	1641.25	11.96	0	1	-814.44
Julian	6	1641.59	12.3	0	1	-814.61
Julian*Rain 1 (Threshold)	8	1642.52	13.23	0	1	-812.95
Julian*Rain 1	8	1642.93	13.64	0	1	-813.15
Rain Avg (Quadratic)	7	1643.22	13.92	0	1	-814.37
Julian*Rain (Threshold)	8	1643.24	13.94	0	1	-813.3
Julian*Rain	8	1643.61	14.32	0	1	-813.49
Julian*Rain 1 (Quadratic)	10	1644.94	15.64	0	1	-811.98
Julian*Rain (Quadratic)	10	1646.08	16.78	0	1	-812.55
Rain 1 (Threshold)	6	1650.27	20.98	0	1	-818.95
Sites+Species	5	1650.82	21.53	0	1	-820.28
Rain Avg	6	1651.06	21.77	0	1	-819.35
Rain (Threshold)	6	1652.21	22.91	0	1	-819.92
Rain	6	1652.91	23.61	0	1	-820.27
Rain 1	6	1652.93	23.63	0	1	-820.28
Rain 1 (Quadratic)	7	1654.52	25.23	0	1	-820.02
Rain (Quadratic)	7	1654.74	25.44	0	1	-820.12

Sites	4	1669.26	39.96	0	1	-830.54
Null	2	1684.75	55.45	0	1	-840.35

Table 3: Forms and measurements of humidity.

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Julian*Hum	8	1626.59	0	0.36	0.36	-804.98
Julian*Hum Avg	8	1628.27	1.67	0.15	0.51	-805.82
Julian*Hum Avg (Threshold)	8	1628.48	1.89	0.14	0.65	-805.93
Julian*Hum Avg (Quadratic)	10	1628.89	2.3	0.11	0.76	-803.96
Julian*Hum (Quadratic)	10	1629.16	2.57	0.1	0.86	-804.09
Julian*Hum (Threshold)	9	1629.33	2.74	0.09	0.95	-805.27
Julian*Hum 1	8	1632.38	5.79	0.02	0.97	-807.87
Hum Avg (Quadratic)	7	1632.7	6.1	0.02	0.99	-809.1
Julian*Hum 1 (Threshold)	9	1634.66	8.07	0.01	1	-807.93
Julian*Hum 1 (Quadratic)	10	1635.85	9.26	0	1	-807.44
Julian (Quadratic)	7	1640.84	14.25	0	1	-813.18
Julian (Threshold)	6	1641.17	14.58	0	1	-814.4
Julian	6	1641.59	15	0	1	-814.61
Hum Avg (Threshold)	6	1644.57	17.98	0	1	-816.1
Hum Avg	6	1645.71	19.11	0	1	-816.67
Hum (Quadratic)	7	1648.68	22.09	0	1	-817.1
Hum (Threshold)	6	1648.82	22.22	0	1	-818.22
Hum	6	1649.43	22.84	0	1	-818.53

Species+Sites	5	1650.82	24.23	0	1	-820.28
Hum 1 (Threshold)	6	1651.29	24.7	0	1	-819.46
Hum 1	6	1651.43	24.84	0	1	-819.53
Hum 1 (Quadratic)	7	1652.96	26.37	0	1	-819.23
Sites	4	1669.26	42.66	0	1	-830.54
Null	2	1684.75	58.15	0	1	-840.35

Table 4: All forms and measurements of seasonal rain.

	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Days Since Above Average Rain	6	1639.36	0	0.64	0.64	-813.5
Days Since Above Average Rain (Quadratic)	7	1640.57	1.21	0.35	0.99	-813.04
Days Since Rain	6	1649.84	10.48	0	0.99	-818.74
Species+Sites	5	1650.82	11.46	0	0.99	-820.28
Days Since Rain (Quadratic)	7	1651.11	11.75	0	1	-818.31
Days Since Rain (Threshold)	6	1651.37	12.01	0	1	-819.5
Days Since Above Average Rain (Threshold)	6	1652.22	12.86	0	1	-819.93
Above Average Rain	6	1652.87	13.51	0	1	-820.25
Above Average Rain (Quadratic)	6	1652.87	13.51	0	1	-820.25
Above Average Rain (Threshold)	6	1652.87	13.51	0	1	-820.25
Sites	4	1669.26	29.9	0	1	-830.54
Null	2	1684.75	45.39	0	1	-840.35

Appendix 3

Table 1: All forms and measurements of temperature.

Temperature	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Min Temp (Quadratic)	7	853.68	0	0.96	0.96	-419.56
Julian*Min Temp (Quadratic)	11	859.97	6.29	0.04	1	-418.32
Min Temp (Threshold)	6	868.53	14.84	0	1	-428.06
Min Temp Avg (Threshold)	6	868.53	14.84	0	1	-428.06
Min Temp	6	869.82	16.13	0	1	-428.7
Julian*Min Temp	9	873.85	20.16	0	1	-427.47
Julian*Min Temp (Threshold)	9	874.5	20.81	0	1	-427.8
Min Temp 1 (Quadratic)	7	877.19	23.5	0	1	-431.32
Julian*Min Temp 1 (Quadratic)	10	878.85	25.17	0	1	-428.87
Mean Temp (Quadratic)	7	879.15	25.46	0	1	-432.3
Julian*Max Temp Avg	8	880.45	26.77	0	1	-431.87
Julian*Max Temp Avg (Threshold)	8	880.64	26.96	0	1	-431.96
Julian *Min Temp Avg (Quadratic)	10	883.63	29.95	0	1	-431.26
Min Temp 1 (Threshold)	6	883.68	29.99	0	1	-435.63
Mean Temp 1 (Quadratic)	7	883.79	30.11	0	1	-434.62
Max Temp 1 (Quadratic)	7	884.07	30.38	0	1	-434.76
Max Temp 1	6	884.14	30.45	0	1	-435.86
Min Temp 1	6	884.22	30.53	0	1	-435.9
Max Temp 1 (Threshold)	6	884.35	30.66	0	1	-435.97
Min Temp Avg	6	884.38	30.7	0	1	-435.98
Min Temp Avg (Quadratic)	7	885.42	31.74	0	1	-435.43
Julian *Mean Temp Avg (Quadratic)	10	885.68	31.99	0	1	-432.29
Mean Temp (Threshold)	6	885.9	32.22	0	1	-436.74
Mean Temp Avg (Threshold)	6	885.9	32.22	0	1	-436.74
Sites+Species	5	886.14	32.46	0	1	-437.92
Mean Temp	6	886.22	32.53	0	1	-436.9
Julian*Max Temp	8	886.95	33.26	0	1	-435.12
Julian*Max Temp (Threshold)	8	886.95	33.26	0	1	-435.11
Max Temp Avg	6	887.43	33.74	0	1	-437.51
Julian (Quadratic)	7	887.47	33.78	0	1	-436.46
Julian *Min Temp Avg	8	887.68	34	0	1	-435.48

Julian *Min Temp Avg (Threshold)	8	887.73	34.05	0	1	-435.51
Julian*Min Temp 1	8	887.75	34.07	0	1	-435.52
Mean Temp 1	6	887.85	34.17	0	1	-437.72
Julian*Min Temp 1 (Threshold)	8	887.88	34.2	0	1	-435.58
Mean Temp 1 (Threshold)	6	887.96	34.27	0	1	-437.77
Mean Temp Avg	6	888.05	34.36	0	1	-437.82
Julian	6	888.11	34.43	0	1	-437.85
Julian (Threshold)	6	888.14	34.46	0	1	-437.86
Max Temp	6	888.17	34.48	0	1	-437.88
Max Temp (Threshold)	6	888.19	34.51	0	1	-437.89
Max Temp Avg (Threshold)	6	888.19	34.51	0	1	-437.89
Julian*Max Temp Avg (Quadratic)	10	888.28	34.6	0	1	-433.59
Julian*Max Temp 1 (Threshold)	8	888.28	34.59	0	1	-435.78
Julian*Max Temp 1	8	888.29	34.6	0	1	-435.79
Max Temp (Quadratic)	7	888.85	35.16	0	1	-437.15
Mean Temp Avg (Quadratic)	7	889.13	35.45	0	1	-437.29
Max Temp Avg (Quadratic)	7	889.31	35.63	0	1	-437.38
Julian*Max Temp (Quadratic)	10	889.49	35.8	0	1	-434.19
Julian*Mean Temp	8	889.53	35.84	0	1	-436.4
Julian*Mean Temp (Threshold)	8	889.53	35.85	0	1	-436.41
Julian*Mean Temp (Quadratic)	10	889.6	35.92	0	1	-434.25
Julian*Mean Temp 1	8	891.86	38.18	0	1	-437.57
Julian*Mean Temp 1 (Threshold)	8	891.86	38.18	0	1	-437.57
Julian*Max Temp 1 (Quadratic)	10	892.41	38.72	0	1	-435.65
Julian*Mean Temp 1 (Quadratic)	10	893.2	39.51	0	1	-436.05
Julian *Mean Temp Avg (Threshold)	8	894.3	40.62	0	1	-438.79
Julian *Mean Temp Avg	8	894.94	41.26	0	1	-439.11
Sites	4	901.07	47.38	0	1	-446.44
Null	2	906.49	52.81	0	1	-451.22

Table 2: All forms and measurements of rain.

Rain	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Rain Week Avg (Threshold)	6	867.81	0	0.9	0.9	-427.7
Rain Week Avg (Quadratic)	7	872.4	4.58	0.09	0.99	-428.92
Julian*Rain Avg (Quadratic)	10	878.38	10.57	0	1	-428.64
Rain Week Avg	6	879.86	12.04	0	1	-433.72
Rain 1	6	886.06	18.25	0	1	-436.82
Species+Sites	5	886.14	18.33	0	1	-437.92
Rain	6	887.16	19.35	0	1	-437.37
Julian (Quadratic)	7	887.47	19.66	0	1	-436.46
Rain (Quadratic)	7	888.03	20.21	0	1	-436.74

Julian	6	888.11	20.3	0	1	-437.85
Julian (Threshold)	6	888.14	20.33	0	1	-437.86
Rain (Threshold)	6	888.24	20.43	0	1	-437.91
Julian*Rain (Threshold)	8	890.14	22.32	0	1	-436.71
Julian*Rain	8	890.18	22.37	0	1	-436.73
Sites	4	901.07	33.26	0	1	-446.44
Null	2	906.49	38.68	0	1	-451.22

Table 3: All forms and measurements of humidity.

Humidity	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Hum (Threshold)	6	873.41	0	0.36	0.36	-430.5
Julian*Hum 1 (Quadratic)	10	874.3	0.9	0.23	0.59	-426.6
Hum	6	875.15	1.75	0.15	0.74	-431.37
Julian*Hum	8	876.51	3.1	0.08	0.82	-429.9
Hum Week Avg (Threshold)	6	877.6	4.19	0.04	0.86	-432.59
Hum Week Avg	6	877.98	4.58	0.04	0.9	-432.78
Julian*Hum Week Avg	8	878.36	4.95	0.03	0.93	-430.82
Julian*Hum Avg (Threshold)	8	878.49	5.08	0.03	0.96	-430.89
Hum Week Avg (Quadratic)	7	878.53	5.12	0.03	0.98	-431.99
Julian*Hum Week Avg (Quadratic)	10	879.92	6.51	0.01	1	-429.41
Species+Sites	5	886.14	12.73	0	1	-437.92
Julian (Quadratic)	7	887.47	14.06	0	1	-436.46
Julian	6	888.11	14.71	0	1	-437.85
Julian (Threshold)	6	888.14	14.74	0	1	-437.86
Julian*Hum (Quadratic)	10	888.82	15.42	0	1	-433.86
Sites	4	901.07	27.66	0	1	-446.44
Null	2	906.49	33.09	0	1	-451.22
Julian*Hum 1	8	2926.25	2052.84	0	1	-1454.77
Julian*Hum 1 (Threshold)	8	2928.18	2054.77	0	1	-1455.73
Hum 1 (Threshold)	6	2972.32	2098.91	0	1	-1479.95
Hum 1 (Quadratic)	7	2973.5	2100.09	0	1	-1479.47
Hum 1	6	2973.83	2100.43	0	1	-1480.71

Table 4: Forms and measurements of seasonal average rain.

	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Days Since Above Average Rain	6	866.36	0	0.69	0.69	-426.98
Days Since Above Average Rain (Quadratic)	7	867.98	1.62	0.31	1	-426.71
Days Since Rain	6	880.59	14.22	0	1	-434.09
Days Since Rain (Threshold)	6	881.05	14.69	0	1	-434.32
Days Since Rain (Quadratic)	7	881.93	15.56	0	1	-433.69
Days Since Above Average Rain (Threshold)	6	884.27	17.9	0	1	-435.93
Species+Sites	5	886.14	19.77	0	1	-437.92
Above Average Rain	6	886.94	20.58	0	1	-437.26
Above Average Rain (Quadratic)	6	886.94	20.58	0	1	-437.26
Above Average Rain (Threshold)	6	886.94	20.58	0	1	-437.26
Sites	4	901.07	34.7	0	1	-446.44
Null	2	906.49	40.13	0	1	-451.22

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